A REDESCRIPTION OF THE BATHONIAN RED ALGA *SOLENOPORA JURASSICA* FROM GLOUCESTERSHIRE, WITH REMARKS ON ITS PRESERVATION

by T. L. HARLAND *and* H. S. TORRENS

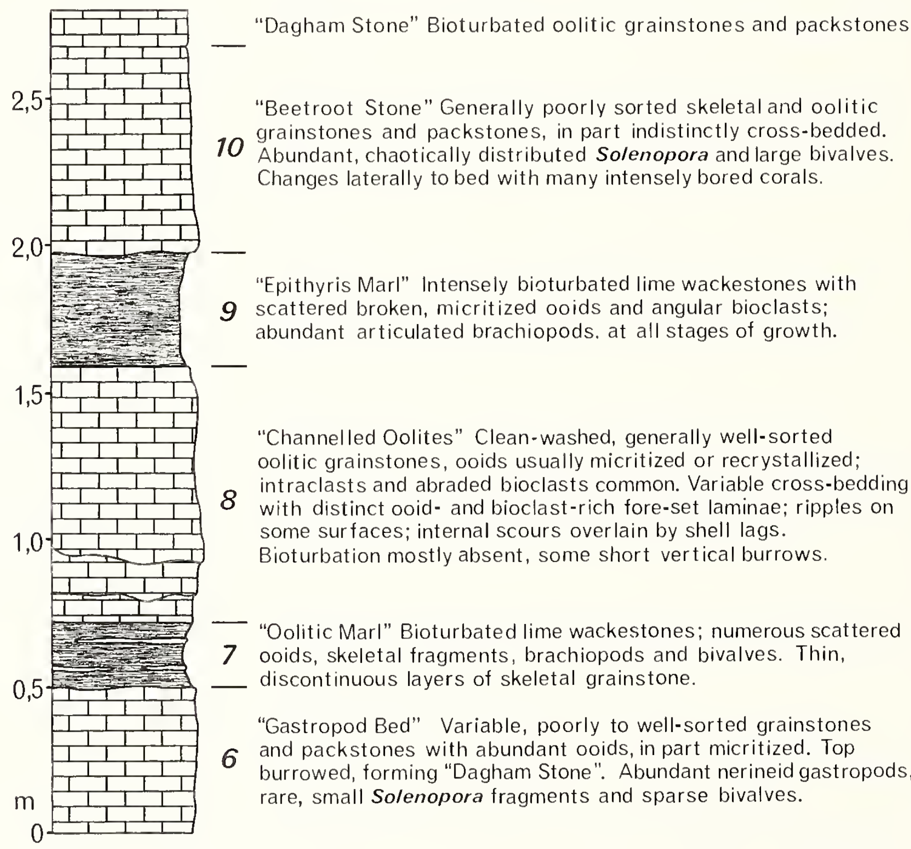
ABSTRACT. The Bathonian red alga *Solenopora jurassica* Brown 1894 ex Nicholson MSS. is redescribed and a neotype designated. It is composed of radiating filaments (0·45 mm mean diameter) divided into cells varying in length between 0·07 and 0·04 mm by concave outward septa. An alternation of layers with well-preserved and poorly preserved tissue structure respectively is typical, and parts of all specimens exhibit a bright pink banding, which is interpreted as remnants of an original pigment. Preservation of this pigment probably depended upon rapid burial of the alga while still alive or very soon after death. The only partial preservation of the pigment is related to variations of the algal tissue, which controlled later leaching.

STRIKING pink-coloured fossils from the White Limestone Formation (Bathonian) near Chedworth in Gloucestershire have been famous since they were first reported by Harker (1890, pp. 89-90) in railway sections provided by the excavation of Aldgrove cutting between Cirencester and Gloucester. Initially, these were not fully named, though they were soon identified by H. A. Nicholson as *Solenopora* Dybowski (*in* Woodward 1894, p. 290). In 1894 Brown, Nicholson's assistant, was the first to present good evidence that the specimens were fossil algae (Nicholson thought *Solenopora* to have been a 'curious extinct hydrozoan') and, using Nicholson's manuscript name, described the new species as *S. jurassica*. However, Brown differed from Nicholson in his assessment of the species. In manuscript Nicholson had seemingly only referred material from Chedworth to *S. jurassica* (see Garwood 1913, p. 469), whereas Brown extended the species to include Corallian (Upper Jurassic) material from around Malton in Yorkshire, and actually figured both a longitudinal section from Chedworth (Brown 1894, fig. 4) and a tangential section from Malton (Brown 1894, fig. 5) when erecting his species. Later, Rothpletz (1908) noted a variation in structural detail between specimens from these two horizons and areas, and proposed the genus *Solenoporella* for the Yorkshire material. This was also the opinion of Garwood (1913, p. 470), who stated, '*S. jurassica* from Chedworth represents a true species of *Solenopora* showing closely packed cells with polygonal outline in tangential section; *S. jurassica* from Malton and elsewhere in Yorkshire has distinctly circular outline in tangential section and is specifically if not generically distinct and is that described by Rothpletz as *Solenoporella*.' However, Lemoine (1928, p. 407) believed these claims to be erroneous and that *Solenoporella* Rothpletz was based on oblique rather than tangential cell cross-sections, but she unfortunately compounded the confusion by referring to Chedworth as being in Yorkshire! None of the material has been examined since this, though the material from Yorkshire, which is often silicified and poorly preserved, is presently referred to the genus *Solenoporella* Rothpletz (Dr. J. K. Wright, pers. comm. 1980). Here we redescribe *Solenopora jurassica* Brown using material only from Chedworth in Gloucestershire, resolve the problem of the unknown numbers of syntypes (now lost) from different horizons by designating a neotype, and also discuss the implications and the possible origin of the pink coloration typical of this material.

[Palaeontology, Vol. 25, Part 4, 1982, pp. 905-912, pl. 100.]

GEOLOGICAL SETTING

The large disused quarry at Foss Cross (Nat. Grid. Ref. SP 055092) near Chedworth in Gloucestershire is an extension of the former Aldgrove cutting and provides fine sections through the White Limestone Formation (Middle and Upper Bathonian). The algae under discussion here were all collected from a single bed near the top of the section at a western promontory of the quarry face, where its abundance and conspicuous pink colour led former quarrymen to term the bed 'Beetroot Stone' (text-fig. 1). Cope *et al.* (1980, p. 35, fig. 6*a*) place these beds in the Hodsoni Zone (basal Upper Bathonian) on the basis of ammonites collected both lower in this section and in the immediate district. These beds (6–11) are lateral equivalents of part of the Ardley Member further east in Oxfordshire described by Palmer (1979). Palmer (1979, p. 204) also notes that in Oxfordshire *S. jurassica* Brown is more common in the stratigraphically lower Shipton Member. The sequence at Foss Cross is dominated by cross-stratified lime sands composed primarily of ooliths and abraded skeletal material (text-fig. 1). Channelling and scouring is commonly observed and bioturbation frequently decreases downward from the tops of thick units (cf. Palmer 1979, p. 224). Deposition appears thus to have been in a predominantly moderate-to-high-energy shoaling environment where much sediment movement occurred relatively rapidly, perhaps during major storms. At other times everyday wave and current energy modified the substrate by rippling and a frequently abundant infauna colonized the higher parts of the sediment. The thin units of lime mud and shelly lime mud included in the sequence (text-fig. 1) reflect prolonged periods of low-energy deposition, probably in extensive, sheltered depressions.



TEXT-FIG. 1. Relevant part of the sequence at Foss Cross Quarry showing sedimentary character and position of the 'Beetroot Stone', logged in metres. Bed numbers (6–10) follow Torrens (1969).

SYSTEMATIC DESCRIPTION

Class RHODOPHYCEAE
Subclass FLORIDEAE
Order CRYPTONEMIALES Schmitz 1892
Family SOLENOPORACEAE Pia 1927
Solenopora jurassica Brown 1894

Plate 100

Type material. Brown's species was based on an unknown number of syntypes from both Chedworth and Malton, varying in size from 'a marble to that of an orange or even larger'. As noted in the introduction, the illustrations accompanying his descriptions comprise a longitudinal section from Chedworth and a tangential section from Malton, both prepared from thin sections. According to Brown his material came from Nicholson's collections. Unfortunately the H. A. Nicholson collection held by Aberdeen University was never properly curated (Benton and Trewin 1978), and consequently the status of all the surviving specimens there is now wholly uncertain. The only surviving material of *S. jurassica* Brown which could constitute syntype material consists of two samples (Aberdeen Univ. Nos. 10676–10677) from a single hand specimen *labelled* as from Malton, Yorkshire, and three thin sections (Aberdeen Univ. Nos. 02809–02811) labelled as from Chedworth, all in a hand other than Nicholson's own (Benton 1979, p. vii). The hand specimens, which, it should be noted, are far more similar to *in situ* material from Chedworth than to that from Malton, and may thus have had labels transposed, have no cut surfaces and show no sign of having provided thin sections. Garwood (1913) also implies that specimens from Chedworth and Malton had been confused. The surviving thin sections prepared from lost Chedworth hand specimens possibly provided the basis for Brown's figure 4 (though no direct match has been made by us) but, if the labelling is correct, they cannot have contributed to Brown's figure 5, based on Malton specimens. In view of Brown's original use of material from two localities, the uncertain authenticity of all material surviving in Aberdeen, the lack of proven syntypes in any other collection examined, and the fact that *S. jurassica* Brown is the first solenoporacean to have been described from Jurassic rocks, the only satisfactory solution is to designate a neotype and provide a redescription and illustrations, and to do this in accordance with Nicholson's apparent original intention, that is, to derive the neotype from the Chedworth exposures.

Originally, the exposures at Chedworth consisted solely of the railway cutting at Aldgrove, which was measured and described by Richardson (1911, p. 107), but in the 1920s Foss Lime and Limestone Co. Ltd. extended the exposure by excavation of Foss Cross quarry, of which the earliest section was again provided by Richardson (1930, p. 270). The quarry was closed in the 1960s and the section along the western side is now protected by the Nature Conservancy as a site of special scientific interest. The material used by us was all collected from this protected section, where it is abundant in the equivalent bed (Richardson 1930, p. 270; Barker 1976, figs. 1–22) to that in the cutting which yielded Harker's and Nicholson's material and some of Brown's syntypes.

Neotype. A single polished specimen (BMNH V 60738) now deposited in the British Museum (Natural History) with four other hand specimens (BMNH V 60739–60742) which all derived from a single large alga during preparation of thin sections. Eight of these (BMNH V 60743–60750) and two other thin sections (BMNH V 60751–60752) from other specimens are also deposited in the British Museum (Natural History). The material was collected from an inverted position in the lower part of the 'Beetroot Stone' (Bed 10 of Torrens 1969) of the White Limestone Formation at Foss Cross.

Diagnosis. Solenopora exhibiting marked banding of alternating layers with well-differentiated and poorly differentiated structure; structure consisting of radiating filaments (cell columns); filaments 0·045 mm mean diameter, filament walls approximately 0·008 mm wide, and cells varying in length between 0·07 and 0·04 mm, separated by outward-concave cell walls 0·005 to 0·008 mm wide.

Description. The alga is well preserved though some areas of the growths have suffered recrystallization. A large size-range is present from rounded or ragged fragments as small as 1 cm diameter to complete though often overturned large hemispherical masses 25–30 cm basal diameter and up to 20 cm high. Occasionally the alga is seen encrusting small corals. Colour banding is characteristic, with reddish-pink, pink, or pale pink bands alternating with buff or off-white bands (Pl. 100, fig. 1). The pink coloration usually fades towards the outer parts of the masses. The alternating bands are usually of the order of 3–6 mm in width but occasionally much finer

(Pl. 100, figs. 1, 2). Numerous variably sized borings are present in the growths, the larger examples infrequently containing *in situ Gastrochaena* sp. or '*Lithophaga*' sp. bivalves, and the surfaces of the algal colonies are often encrusted by oysters, bryozoans, and serpulids. Distortion of algal cell structure is seen in several areas beneath encrusting organisms but this is not always the case. In addition to the epifauna the colonies usually have a crusting of coarse skeletal sediment and clean natural surfaces are rarely encountered. Many of the features described below from thin sections, including the characteristic radiating filaments, can also be distinguished in broken or worn hand specimens.

In thin section the closely packed filaments (cell columns) are seen to radiate from the lower areas upwards and outwards to the exterior; the filaments are generally straight or slightly curved (Pl. 100, figs. 4, 6) but exceptions are common, particularly near the bases of growths and around sediment incursions where the structure may be chaotic and the filaments contorted. Cross-sections show the filaments to be most commonly adpressed, forming regular hexagonal to irregularly polygonal patterns (Pl. 100, figs. 5, 7) but they may also be loosely packed, in which case they have approximately circular cross-sections; all patterns can be and usually are present within the larger growths. The cells are mostly filled with calcite spar and differentiation between them and dark wall material is simple. Where micritic sediment infills the cells some difficulty is experienced in delimiting this from wall material. Mean diameter of filaments mid-wall to mid-wall, 0·045 mm (observed range 0·029 to 0·059 mm); mean cell diameter 0·039 mm (observed range 0·024 to 0·056). Thickness of wall material is from 0·001 to 0·02 mm, although these are rare extremes (the former noted in a specimen shown by deformed sediment-filled borings to have undergone post-mortem crushing and the latter in the lower, chaotic parts of one specimen); mean thickness of wall material 0·008 mm (usual range 0·005 to 0·01 mm), and shows slight irregularities along its length. The walls nowhere exhibit any internal structure.

In vertical section the characteristic banding is clearly seen to arise from the alternation of layers with well-defined structure dominated by filament walls (Pl. 100, figs. 4, 6, 8) and layers with poorly defined structure where filament walls are inconsistent (Pl. 100, figs. 3, 6). Pink colour most commonly corresponds with layers of poorly defined structure. Mostly, the filaments run adjacent and are approximately parallel to each other; bifurcation is quite frequent but is inconspicuous, occurring randomly and sparsely throughout the body of the growths. The medium-sized and larger masses usually include elongate sediment-filled 'cracks' several centimetres long, up to 0·5 cm wide and oriented perpendicular to the banding (Pl. 100, fig. 1). Adjacent filaments curve gently towards these 'cracks', which are not borings but features of the original growth form. Banding is seen deflected downwards towards these features, indicating that the upper surface during growth was mammillated. The filaments are divided into cells by frequent cell walls which are gently outward-concave (Pl. 100, fig. 8). Cell walls are composed of the same material as filament walls but are generally slightly thinner, ranging from 0·004 to 0·01 mm. The cell walls divide the filaments into discrete cells 0·07 to 0·04 mm (most usually 0·07 to 0·25 mm) long. In layers where the stucture is well defined, cell walls in adjacent filaments are

---

EXPLANATION OF PLATE 100

Polished slab and photomicrographs of *Solenopora jurassica* Brown from the 'Beetroot Stone' at Foss Cross quarry, Chedworth. All specimens in the British Museum (Natural History), London.

Fig. 1. Slab showing polished surface of neotype, which shows the typical colour banding and 'cracks' widening into more deeply coloured bands. Also note sediment incursions (arrowed). Numbered scale in cm. BMNH slide V 60738.

Fig. 2. Longitudinal section from neotype, showing tissue banding. ×14. BMNH slide V 60743.

Fig. 3. Longitudinal section, showing grid-like nature of tissue layers with poorly preserved filaments. ×55. BMNH slide V 60752.

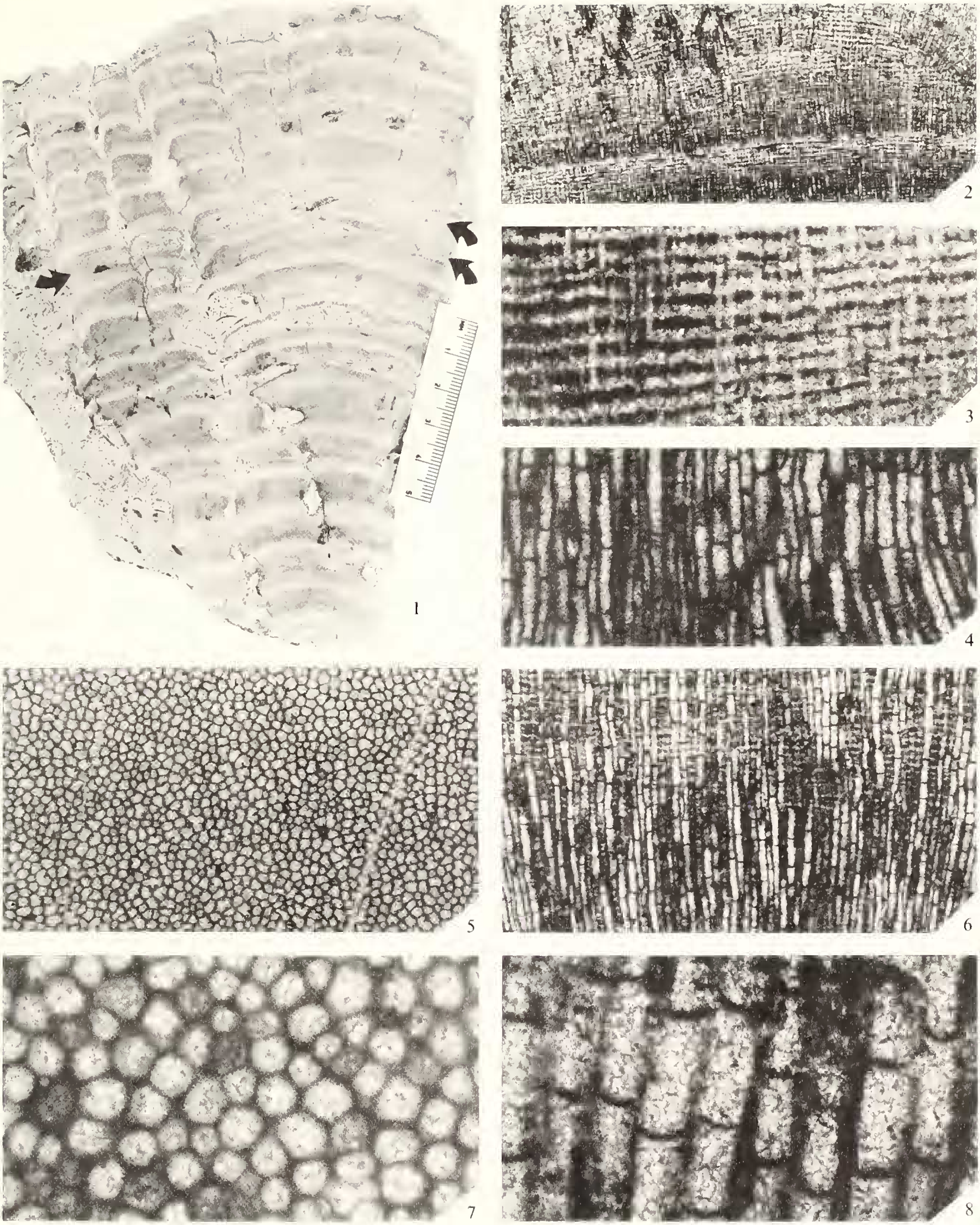
Fig. 4. Longitudinal section, showing nature of tissue layers with well-preserved filaments. ×50. BMNH slide V 60751.

Fig. 5. Transverse section from neotype, showing regular polygonal cell cross-section. ×35. BMNH slide V 60744.

Fig. 6. Longitudinal section from neotype, showing well-preserved filaments changing upwards into layer with less well preserved filaments. ×25. BMNH slide V 60743.

Fig. 7. Transverse section, showing close-up of spar-filled cells. ×120. BMNH slide V 60747.

Fig. 8. Longitudinal section, showing upward-concave divisions dividing filaments into cells. ×150. BMNH slide V 60749.



HARLAND and TORRENS, *Solenopora jurassica* typically randomly placed but occasionally they occur at the same level across several filaments. This contrasts with layers of poorly defined structure, where the septa are often more prominent than tubule walls and frequently occur at the same level across numerous tubules. This results in a grid-like or even concentric appearance. The concentric appearance is also often accentuated by recrystallization along thin layers (0·035 to 0·04 mm thick) which alternate with preserved tissue (Pl. 100, fig. 3). Rare, well-defined filaments or groups of two-to-five filaments pass through these bands and similar groups originate close to the top of the bands and continue upwards into suprajacent bands with well-preserved structure throughout. Smooth irregularities in the banding, in the form of crescentic outgrowths from the top of the bands of poorly defined structure, are common and supplement the mammillated growing surface noted above.

Neither hypothallic tissue (basal layers of unusually large cells) nor reproductive features (sporangia, conceptacles) have been noted.

REMARKS

A number of authors have commented on the presence of a strong pink colour in specimens of *S. jurassica* Brown (e.g. Garwood 1913; Lemoine 1928; Cailleteau 1966) and banding of tissue is known in species of *Solenopora* from the Ordovician until extinction in the late Jurassic (Johnson 1960, 1961, 1963, 1964). Lemoine (1928, p. 406) suggested that the pink colour was an original feature, preserved by rapid burial of live algae. Work in progress by the authors and others has so far confirmed the presence of organic pigments and suggests that they are probably porphyrins. Further analyses are being performed in an attempt to ascertain the exact compounds involved.

Sediments comprising the White Limestone Formation to the east of Chedworth were deposited in a complex mosaic of shallow subtidal and occasionally intertidal or supratidal environments developed on or near the London Platform, between the north-easterly London Land Mass and the offshore, deeper-water south-westerly Severn Basin (Palmer 1979). Beds composed of abundant *in-situ* or storm-disrupted coral colonies are common throughout the White Limestone in that area, and Palmer (1979, p. 213) likens those found in Oxfordshire to modern *Porites* shoals and thickets present in shallow water (about 3 m depth) in the Florida Keys. He also notes the lack of algae in the Oxfordshire coral beds when compared to their modern equivalents, where *Goniolithon* (Rhodophyceae) and *Halimeda* (Chlorophyceae) are common, and suggests this exclusion results from high water-turbidity caused by suspended fines from the nearby London Land Mass. However, reports of algae in the White Limestone further west are much more common (e.g. Richardson 1930, 1933; Torrens 1967; Elliott 1975). As noted above, the sedimentary character of the sequence in which *S. jurassica* Brown occurs at Foss Cross (text-fig. 1) and of the White Limestone as a whole in the area around Chedworth is indicative of variable high-to-moderate-, occasionally low-, energy conditions and an environment of intermittently shifting variable skeletal substrates, which were often oolite-rich, cut by storm-generated and storm-maintained channels or scours (cf. Klein 1965; Fürsich and Palmer 1975; Silva 1976). This indicates that the Chedworth area was sited at the edge of the London Platform shelf, where higher energy levels and greater water exchange resulted in reduced turbidity and permitted a more profuse flora and the local development of algal shoals. Ware and Windle (1981) describe a similar, slightly shallower situation for the overlying Forest Marble Formation near by. Within this sedimentary framework it is easy to envisage storm or tidal current disruption of benthic organisms and their rapid burial in channels or beneath migrating shoals, and we interpret the 'Beetroot Stone' at Foss Cross as one such storm-disrupted and rapidly buried algal shoal. The *Solenopora* themselves also suggest disruption and rapid burial. Direction of growth is shown clearly by the banding, and counts indicate that at least 62% of studied specimens (*c.* 50) were preserved in an orientation other than that of life. Borings and particularly epifauna are, however, concentrated on the upper parts (life orientation) of the algal masses. Large bivalve and other irregular borings were only noted into the upper growth surfaces of specimens and many of the smaller, thin tubular borings (?*Trypanites*) are seen to originate within the masses at marked growth lines, indicative of overgrowth by tissue, that is, formation during growth. Encrusting oysters and serpulids have again only been noted on the same tops or upper sides of specimens and, although several have been noted spreading along the sides and basal parts of masses, the majority of bryozoan encrustations are also concentrated at the tops of masses. This evidence, together with their very large size range and chaotic sorting, supports the idea of disruption and a rapid and total burial, killing the alga, preserving the original pigment and preventing further colonization by boring or encrusting organisms.

The alternating bands of colour closely correspond with variations in the structure of the algae, the pink bands relating to layers of tissue with poorly defined structure. It seems possible that the colour banding originated during the life of the alga and Lemoine (1911) has suggested that colouring matter is produced in living algae more abundantly at some times than others, though not necessarily relating to distinct growth phases. However, several features observed in the Chedworth specimens argue against this. First, although the pinkish coloration relates most commonly to the bands of poorly defined tissue, this is not always the case. Secondly, even within these bands there is usually a fading of the colour towards the perimeters of the masses. This strongly indicates that the whole of the algal masses were originally coloured and that subsequent leaching has taken place around the edges of the buried masses. Leaching has also taken place along the sides of the 'cracks' noted in the earlier description, as again the colour fades towards these features. The distribution of preserved pigment can thus be best explained as follows: leaching preferentially removed original pigment from the perimeters of the masses and along sediment-filled 'cracks' or borings and also from layers of tissue with well-defined radial structure which were more porous. The more compact, concentric arrangement within the layers of tissue with poorly defined structure coupled with preferential recrystallization significantly reduced porosity in these layers and served to decelerate or prevent leaching. The origin of the differentiation of the algal tissue into these alternating bands is unknown but it is tempting to propose a seasonal influence. Whatever the cause, this alternation of tissue appears to be the prime factor in the preservation of the original pigmentation after burial of the alga.

Acknowledgements. We gratefully acknowledge help from Drs. G. F. Elliott, P. D. Lane, and T. J. Palmer, who each suggested improvements to our original manuscript. Joan Cliff typed the final manuscript and David Kelsall produced photographs for the plate.

REFERENCES

BARKER, M. J. 1976. A stratigraphical, palaeoecological and biometrical study of some English Bathonian Gastropoda (especially Nerineacea). Ph.D. thesis, University of Keele (unpubl.). 2 vols.

BENTON, M. J. 1979. H. A. Nicholson (1844–1899), invertebrate palaeontologist: bibliography and catalogue of his type and figured material. *R. Scott. Mus. Info. Series, Geol.*, **7,** 94 pp.

—— and TREWIN, N. H. 1978. Catalogue of the type and figured material in the Palaeontology Collection, University of Aberdeen. *Publ. Dept. Geol. Min. Univ. Aberdeen*, **2,** 28 pp.

BROWN, A. 1894. On the structure and affinities of the genus *Solenopora*, together with descriptions of new species. *Geol. Mag.* (4), **1,** 145–151 and 195–203.

CAILLETEAU, P. 1966. Découverte d'un gisement à Solénopores dans le Jurassique supérieur de la Tour de Scay. *Ann. sci. de l'Univ. Besançon*, 3rd Ser., *Géol.* **2,** 59–60.

COPE, J. C. W. *et al.* 1980. A correlation of Jurassic rocks in the British Isles, Part Two. Middle and Upper Jurassic. *Geol. Soc. Lond. Spec. Rep.* **15.** 109 pp.

ELLIOTT, G. F. 1975. Transported algae as indicators of different marine habitats in the English Middle Jurassic. *Palaeontology*, **18,** 351–366.

FÜRSICH, F. T. and PALMER, T. J. 1975. Open crustacean burrows associated with hardgrounds in the Jurassic of the Cotswolds, England. *Proc. Geol. Ass.* **86,** 171–181.

GARWOOD, E. J. 1913. Presidential address, Section C. *Rept. British Assoc. for 1913*, 453–472.

HARKER, A. 1890. On the sections in the Forest Marble and Great Oolite formations exposed by the new railway from Cirencester to Chedworth. *Proc. Cotteswold Nat. Fld Club*, **10,** 82–93.

JOHNSON, J. H. 1960. Paleozoic Solenoporaceae and related red algae. *Colo. Sch. Mines Q.* **55,** 1–77.

—— 1961. *Limestone-building algae and algal limestones.* 297 pp. Colorado School of Mines, Golden.

—— 1963. Pennsylvanian and Permian algae. *Colo. Sch. Mines Q.* **58,** 1–211.

—— 1964. The Jurassic algae. Ibid., **59,** 1–129.

KLEIN, G. de V. 1965. Dynamic significance of primary structures in the Middle Jurassic Great Oolite Series, Southern England. *Soc. Econ. Paleont. Mineral. Sp. Publ.* **12,** 173–191.

LEMOINE, P. 1911. Structure anatomique des Mélobesiées. Application à la classification. *Ann. Inst. Océanogr. Monaco*, **2**, 1-215.
—— 1928. Les *Solenopora* du Jurassique de France. *Bull. Soc. géol. Fr.*, sér. 4, **27**, 405-417.
PALMER, T. J. 1979. The Hampen Marly and White Limestone formations: Florida-type carbonate lagoons in the Jurassic of central England. *Palaeontology*, **22**, 189-228.
RICHARDSON, L. 1911. On the sections of Forest Marble and Great Oolite on the railway between Cirencester and Chedworth, Gloucestershire. *Proc. Geol. Ass.* **22**, 95-115.
—— 1930. The Fosse Lime and Limestone quarry and works. *Proc. Cotteswold Nat. Fld Club*, **23**, 269-272.
—— 1933. The country around Cirencester. *Mem. geol. Surv. Eng. Wales*, Sheet **235**. 119 pp.
ROTHPLETZ, A. 1908. Über Algen und Hydrozoen im Silur von Gotland und Oesel. *K. svensk. vetensk. akad. Handl.* **43**, 1-23.
SILVA, L. I. 1976. Litofacies del Bathoniano en el area de Cirencester (Gloucester), Inglaterra. *Primer Congreso Geol. Chileno*, **1**, C41-C56.
TORRENS, H. S. 1967. The Great Oolite Limestone of the Midlands. *Trans. Leicester Lit. and Phil. Soc.* **61**, 65-90.
—— 1969. *Guides to Field Excursions from London. Int. Field Symp. on the British Jurassic*, Keele University. 35+3 pp.
WARE, M. and WINDLE, T. M. F. 1981. Micropalaeontological evidence for land near Cirencester, England, in Forest Marble (Bathonian) times: a preliminary account. *Geol. Mag.* **118**, 415-420.
WOODWARD, H. B. 1894. The Jurassic rocks of Britain, vol. 4. The Lower Oolitic rocks of England (Yorkshire excepted). *Mem. Geol. Surv. U.K.* 628 pp.

T. L. HARLAND and H. S. TORRENS
Department of Geology
University of Keele
Keele
Staffordshire ST5 5BG

Typescript received 4 May 1981
Revised typescript received 16 October 1981